STUDIES IN THE MORPHOLOGY OF THE ASCOMYCETES I. THE STROMA AND THE COMPOUND FRUCTIFICATION OF THE DOTHIDEACEAE AND OTHER GROUPS

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The morphology of the ascocarp has been a subject of continued investigation since the time of deBary and his contemporaries when the discovery was made that specially differentiated hyphae, called by Fuisting (29) "Woronin's hyphae" originate the ascogonia from which the asci arise, and from the stalks of which the perithecia are built. It appears that Janczewski (41) was the first to fully establish the origin of the asci in his studies on *Ascobolus,* but it remained for Harper (34) and later workers to establish by cytological methods the morphological significance of these structures. On the other hand the morphological characteristics and homologies of the various ascocarp aggregates or compound fructifications that are so well represented in the Pyrenomycetes are in need of much further study. These clusters or compounds of ascocarps are to be distinguished sharply of course from those cases in which the ascocarp itself arises in connection with a cluster of ascogonia as in *Pyronema, Ascodesmis, Thecotheus,* etc., as shown by the Tulasnes, Harper (35), Claussen (18), and Overton (55) respectively. Here the ascocarpic unit is itself a compound as compared with those cases in which, as in the powdery mildews, it arises in connection with a single ascogonium.

The structure of these complex fruiting bodies is extremely

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variable as shown by deBary (6) and later by numerous taxono-
mists who have worked with these forms. Several attempts have
been made to define the various structures encountered in the
many subdivisions of the group and a confusing terminology has
arisen. Before such confusion can be eliminated careful com-
parative studies must be made to establish the relationship of the
various structures on the basis of their homologies. Such studies
have established already the types of the perithecial wall in a num-
ber of specific cases as Boudier (12) for instance has done in the
Discomycetes where he goes into great detail in describing the ex-
ternal structure of the apothecium which may be glabrous,
furfuraceous, tomentose or pilose. The origin and characters of
these various superficial outgrowths are also of diagnostic im-
portance according to Boudier.

In such simple ascocarps as the cleistocarps of the Erysiphaceae
the wall consists from the inside out of nurse cells, protective and
more or less hardened, probably chitinized cells, and appendages
of various sorts.

The development of fleshy or carbonized structures which are
commonly known as stromata, sclerotia, etc., in which the as-
cocarps are embedded or from which they arise, present as noted
further problems as to the nature and methods of origin of such
aggregate fructifications.

The association in many cases of conidial fructifications, with
or preceding the ascocarps, which present many parallel forms
to the ascogenous fructifications add further complications and
to make matters still more complex the physiological effect of
parasitism runs through all the groups.

The presence or absence of stromata has been long regarded as
a basis for the delimitation of systematic groups of major rank
but it seems to me clear that with increasing knowledge this usage
is quite indefensible since in many cases it separates what are
obviously on phylogenetic grounds closely related species. As
the subject is of prime importance for the proper morphological
grouping of the subdivisions of the ascomycetes especially, I have
thought it worth while to bring together and comment upon the
current practice of students of the group in this particular.

For the Dothideaceae, which have been given family rank in the

Pyrenomycetes by Fuckel (28), Winter (83) and others, and ordinal rank by Lindau (49) and Theissen and Sydow (73) in their more recent revision of these forms, the chief diagnostic characters given by most systematists are (1) the presence of a stroma and (2) the development of cavities within this stroma which are pyrenocarp-like but which lack an independent perithecial wall of the usual type.   On the basis of these characters the group has been set apart as distinct from the usual type of Pyrenomycete since the time of Fuckel although several investigators, notably von Hohnel (38), Winter (loc. cit.) and Theissen and Sydow (loc. cit.), have called attention to the inadequacy of these characters as a basis for classification inasmuch as all gradations occur between species which develop a stroma with pyrenocarps appearing merely as locules without well differentiated perithecial walls (*Catacauma*) and other species which on the one hand develop definite stromata enclosing pyrenocarps with well differentiated walls (*Nummularia, Hypoxylon*), and on the other develop groups of pyrenocarps with well marked walls but no truly stromatic elements or only scanty mycelial aggregations (*Phyllachora graminis*).

As indicated above the Dothideaceae have received quite different treatment at the hands of the systematic mycologists. Fuckel established the family on the grounds that the ascocarps lacked a definite perithecium and were embedded in a stroma. He made the genus *Dothidea* the type of family with *D. gibberulosa* (Ach.) as the type species.

Subsequent workers have clung to these characteristics in the main but have differed rather widely as to the limits of the family. Winter separated the Dothideaceae from the Hypocreaceae and Sphaeriaceae on the ground that the stroma in the Dothideaceae is always present, usually not fleshy, black or blackish-brown, and that perithecia are not formed or if formed are not well differentiated from the stroma.   He included nine genera and thirty-eight species.

Lindau who first raised the group to ordinal rank separated it from the Hypocreales on the consistency of the stroma and from the Sphaeriales on its always possessing a dark colored stroma and lacking a definite perithecium.   He included 25 genera and

over 400 species, of which 200 were included in the genus
Phyllachora. Practically all of the species thus segregated by
Lindau are parasitic.

Theissen and Sydow have increased the number of genera and
species enormously, recognizing 140 genera of which *Phyllachora*
with 322 species is the largest. They have established four fami-
lies as follows: (1) Polystomellaceae: Stromata with radiating
plate-like cover; ascus-stroma arising either superficially and then
with an intramatricular hypostroma or wholly subcuticularly.
Locules linear or circular, variously formed. (2) Dothideaceae:
Stromata of parallel hyphae, prosenchymatous or more or less
parenchymatous, warty or smooth, without a covering structurally
differentiated, developing superficially with an intramatricular
hypostroma. Locules circular, enclosed in the stroma. (3)
Phyllachoraceae: Stromata under the cuticle or epidermis, remain-
ing covered with a cuticular or epidermal clypeus, prosenchymat-
ous dothideoid in structure or of more or less irregular hyphae.
Locules enclosed in the stroma or leaf tissue, connected at the apex
with the clypeus. (4) Montagnellaceae: Locules isolated; de-
veloping either in the mesophyll without stroma or with irregular
hyphal, often entirely reduced vegetative stroma here and there
forcing up the epidermis; or lying on an interwoven perithecium-
like basal stroma; or enclosed in individual stroma-columns.

Their last family especially needs more careful study to deter-
mine its affiliations. The lack of stroma indicates relationships
with the Sphaeriales and the lack of perithecial walls indicates
relationship with the Dothideaceae according to their views.

The whole order consists almost exclusively of leaf parasitic
forms which is rather remarkable and either indicates that the
reduction in structure of the perithecium is associated with par-
asitism or that the saprophytic forms have not been studied so
thoroughly.

Since we are concerned in this study with definite structures,
the terminology of which has been rather loosely applied by the
various students of the Ascomycetes, it is in place to briefly re-
view the usage of these terms and to delimit them in so far as
possible for the presentation to follow.

The earliest use of the term stroma appears in the work of

Persoon (57) who employed it to describe the structures on or in which are borne the pyrenocarps in the genus *Sphaeria*. He made eight divisions of this genus based on variations in the shape, etc., of the stroma.

In his later work, Persoon (58) uses the term only in connection with the "receptaculum" in his group "Sphaeriis" as follows: "In Sphaeriis carnose suberosum est et stroma audit." As examples he includes *Sphaeria militaris* (*Cordyceps*), *Xylaria* spp. and *Hypoxylon* spp. He also uses "receptaculum" for the fructification in the Pezizaceae, for the pileus of Basidiomycetes, etc. From this it is apparent that he considers stroma and receptaculum synonymous but prefers the term stroma for the matrical complex in the Sphaeriaceae.

In the glossary of technical terms S. F. Gray (33) gives the very misleading definition of stromata as "Irregular apothecia in which the sporae are immersed. *Sphaeria*."

Fries' (27) usage of the term is also essentially that of Persoon, *i.e.*, a matrix in which pyrenocarps are imbedded. "Uterus subinduratus, perithecium dicitur, plura stromate communi saepe juncta; nucleus subgelatinosus." He mentions stromata more specifically in connection with the genus *Dothidea* (p. 318).

Leveillé (45) does not use the term stroma but uses receptacle in a synonymous sense. He applies the term conceptacle to the ascocarps in the Hysteriaceae, Phacidiaceae, and Sphaeriaceae.

Berkeley (8) says of the Sphaeriaceae, "The stroma may be developed in varying degrees, being more or less intimately incorporated with the bark, or it may be quite free, assuming various degrees of consistence, and, according to its mode of expansion or elongation, affording very excellent characters. Thus we have the multitude of pustular or stromatic species, which grow on the branches of trees, or on decayed wood; while the more elongated clavate or simply globose forms yield the species of *Hypoxylon* and *Cordyceps*. Some of the most beautiful are those which grow on insects (Ex. *Cordyceps Robertsii* on *Hepialus virescens*)."

Cesati and de Notaris (16) applied the term in the sense of Persoon's later usage to the receptacle. They discuss the vari-

ations in form of the receptacle from the standpoint of its value in the taxonomy of the Sphaeriaceae.

The Tulasnes (77) employ the term stroma for the fructifications in their family Xylariei which form conidia first and after further development, the perithecia. They recognize four types of stromata: (*a*) "stromate fructiculoso" (Ex. *Xylaria polymorpha*, etc.), (*b*) "stromate repando pulvinato" (*Ustulina vulgaris* and *Poronia punctata*), (*c*) "stromate effuso" (*Eutypa* spp.), and (*d*) "stromate pulvinato vel placentiformi" (*Dothidea Ribesia* Fr., *D. melanops* Tul., *Polystigma rubrum* Pers., *Melogramma Bulliardi* Tul., *M. rubricosum* Tul., *M. gastrinum* (Fries) Tul.).

In connection with the family Valsei which includes *Diatrype disciformis, D. Quercina, Quaternaria Persoonii* Tul., *Calosphaeria, Melanconis, Cryptospora and Valsa,* the stroma is mentioned by the Tulasnes only incidentally. Neither do they describe stromata as of diagnostic importance in the species of their family Sphaeriei which include the genera *Cucurbitaria, Massaria, Sphaeria, Pleurostoma, Pleospora,* etc.

In their later volume the Tulasnes (78) treat the Nectriei, Phacidiei and Pezizei. In the Nectriei they include the genera *Torrubia (Cordyceps), Epichloe, Hydnopsis, Hypocrea, Hypomyces, Nectria* and *Sphaerostilbe.* In the genus *Torrubia* they designate the stroma as follows: "*Stroma (Sporidochium* Link.) carnosum nunc in brachia sparsa aut caespitosa, simplicia vel divaricato-ramosa discedit, nunc contra in columellas crassiores, saepius simplices, erectas, sursum claviformes aut capitatas informatur, semper autem e matrice, quaecunque sit, emergit. Pars summa stromatis gracilioris et ramosi in conidia minima, globosa aut breviter linearia, pallida et pulverea fatiscit; columnae validiores ascophorae evadunt." However, in *T. coccigena* Tul. they say " . . . mycelii intestini causa in stroma solidum matatur ex quo flagella et columella fertiles proderunt." *Hypocrea rufa* Tul. possesses stroma but *Hypomyces* only vegetative, more or less loose or flocculent mycelium in its fungous hosts. *Nectria* possess stromata which first give rise to conidia, and upon their surfaces the ascocarps are later produced. *Epichloe typhina* forms a more or less dense fleshy structure with its host tissues and they men-

tion its resemblance to *Claviceps* but they do not call this structure either stroma or sclerotium. *Sphaerostilbe* is like *Nectria* except the conidia are borne on the apex of a column arising from the stroma.

In the Phacidiei, according to the Tulasnes, *Rhytisma* possesses a stroma which is like a sclerotium, covered with a cortex. *Stictis ocellata* (Pers.) Fries has a well developed stroma which first produces conidia from the surface and later the discocarps arise within the stroma. *Phacidium Ilicis* forms its ascogenous stroma from the pycnidial structure.

Certain of the Pezizei as *Cenangium* and *Dermatea* form well developed stromata according to these workers. From the above examples it will be seen that the Tulasnes had very definite ideas as to what constitutes a stroma but that they made taxonomic use of this structure only in their classification of the Xylariei.

An important contribution to our knowledge of the stroma was made by Fuisting (loc. cit.) who carefully investigated the vegetative structures of several Pyrenomycetes, including *Stictosphaeria Hoffmani* Tul., *Diatrype Quercina* Pers., *D. disciformis* Hoffm., *Eutypa lata* Pers., and *Nummularia Bulliardi* Tul. In the last named species he distinguishes as *epistroma* a hyaline pseudo-parenchymatous crust formed in the outer layers of the primary cortex of the host which produces conidia. Under this crust a *hypostroma* is produced later in which the perithecia develop. Ruhland as will be shown later in his use of the terms *ectostroma* and *entostroma* has followed this conception of Fuisting. In my opinion the distinction of *epistroma* and *hypostroma* as made by Fuisting is of real morphological significance and since they are earlier terms and seem from the etymological standpoint to be preferable it would seem that they should supplant Ruhland's terms.

In *Quaternaria Persoonii* Tul. the epistroma is well developed and takes part in the resorption of the periderm. The " Woronin hyphae " develop within this structure. In Fuisting's discussion of *Hypoxylon* and *Xylaria* he employs the term stroma in the sense of its present application to these forms.

In a later paper Fuisting (30) describes *Poikiloderma bufonium* Berk. & Br. which possesses a rudimentary stroma, and *Massaria*

polysarpa, M. rhodostroma, Bathystomum amblyosporum, and *B. circumcissum* which form well developed stromata. The stromata of the two later species are of the diplostromatic type of Ruhland.

Nitschke (54) like the Tulasnes differentiates four types of stromata as follows on the basis of their general form: (*a*) *Xylaria*-stroma, (*b*) *Hypoxylon*-stroma, (*c*) *Diatrype*-stroma and (*d*) *Valsa*-stroma.

Fuckel (loc. cit.) uses the term stroma in the Persoonian sense. He established the family Dothideaceae Nitsch, with the following characterization. " Die Schlauch liegen in, nicht weiter gesonderten, von keiner eigenen Haut umgebenen, Zellen, im Innern des Stromos." He names *Dothidea* Fries as the type genus of which *Sphaeria gibberulosa* Ach. is the type species. It is of interest to note that Fries (26) came to the conclusion that *S. gibberulosa* cited as the type species of *Dothidea* was synonymous with *Arthonia moriformis* Acharius and later in his Systema (27) he cited *D. moriformis* (Ach.) as the type of the genus *Dothidea*. Since it appears that this species is not dothideaceous but probably belongs to the Discomycetes we have the anomalous situation of recognizing the name Dothideaceae when the genus *Dothidea* upon which it was based should be dropped because its type does not conform to the characters established for the family.

An interesting account of the development of the fructification in the asterinoid types has been made by Ward (82) who investigated *Asterina (Dimerosporium) spissa* Syd. According to Ward the disc or radiate plate so characteristic of these forms develops as an outgrowth of one or two hyphal cells. The center of this disc becomes raised by the formation of a closely packed mesh of hyphae which evidently are produced from the under surface of the cells of the disc. Within this mass the primordia appear which in his opinion are made up of ascogenous hyphae, the origin of which is not clear. Ward considers the disc as a stroma.

De Bary's (6) use of the term stroma is again scarcely different from that of Persoon. It is for him a crust or cushion or an erect more or less branched body on which or in which the ascocarps are developed. He goes so far however as to include the disc or saucer shaped fruit bodies of the discomycetous lichens in

the same category.   Stroma and receptacle are for him essentially synonymous.

Goebel (31) defines stroma in the sense of de Bary, but as noted later he is keenly aware of the morphological significance of the stroma and stroma-like structures.

Winter (loc. cit.) in his descriptions of the stroma notes that it is difficult to be sure of its character in cases in which it consists essentially of the more or less modified thickened and blackened substratum.   He would regard the typical stroma as a pseudo-parenchymatous mass in which cavities are hollowed out for the production of asci, these cavities having no differentiated walls. He is explicit in holding that a stroma is present in those forms in which as in *Homostegia Piggotii* (Berk. & Br.) Karst. the pyrenocarps with their perithecial walls are well individualized and lie in a very loose mycelial network, the dense pseudo-parenchymatous material appearing merely as an upper and under crust between which the pyrenocarps lie.   To be excluded from the Dothideaceae are those forms in which the stroma consists of a dense dark rind and a sclerotium-like medulla in which the pyreno-carps are imbedded, the pyrenocarp walls being also sharply dif-ferentiated and separated from the matrix in which they lie.

Brefeld (14) and von Tavel (67) hold that the Pyrenomycetes are the only forms which possess a true stroma.

Ellis and Everhart (23) follow the Persoonian usage of the term.

Jaczewski (40) makes the presence and absence of stroma the basis for dividing the Pyrenomycetes in two groups: (*a*) " Pyreno-mycetes simples," without stroma, and (*b*) " Pyrenomycetes composes," with stroma.   In his usage of stroma he includes forms in which the context consists merely of loose and wefted hyphae as well as those of denser consistency.

In his systematic treatment of the Ascomycetes Lindau (47) considers the fruit body of certain sub-families of the Pezizineae, viz., Cenangiaceae, Cordieritidaceae, Cyttariaceae and Phymato-sphaeriaceae, to be made up, in part at least, of stroma.   He con-siders the fruit bodies of the whole group Phacidineae as having stromatic characters as well as a part of the Hysteriineae.   But he does not define the stroma as found in these groups.

In the Pyrenomycetes, Lindau (48) considers any fleshy structure appearing as a matrix for ascocarp formation as stroma. For the Dothideales he notes: "Gehause typisch von der Stromasubstanz nicht abesetzt, bei einiger nur zum Teil, bei anderen aber deutlich geschieden."

Ruhland (60) has studied quite fully the development and structure of the stromata for a number of the Sphaeriaceae. He distinguishes as *ectostroma* the earlier and more or less vertically developed structure which generally produces the conidia when they are present, and as entostroma the inner and later developed structure which produces ascogonia though he also regards the ectostroma as a direct product of the undifferentiated mycelium which is destined to become the entostroma. Those species like *Diatrype discisformis* (Hoffm.) Fries develop the early stages of the ectostroma within the periderm of the substratum. This is at first a lens-shaped structure which by continued growth at the center becomes cone shaped and ruptures the periderm, a main function of the ectostroma according to Ruhland. From the lateral surface of this cone the conidia are produced after which the outer portion of the cone including the conidial hymenium turns brown and dies. The mycelium from which the ectostroma develops remains meristematic and after conidial production has ceased, hyphae from this layer grow inward to the cortical parenchyma of the host just outside the sclerenchyma layer. These hyphae then spread out tangentially to the host and by dissolving and pushing apart the cells build up a loose cushion-shaped plectenchyma within which the primordia of the several ascocarps develop. From this same entostroma *anlage* which gave rise to the plectenchyma, a further outward and slightly downward growth now takes place. This spreads out into a porous plectenchymatous layer which eventually becomes denser and covers the structure in which the ascocarps are developing. This layer also effectually cuts off the dead outer ectostroma and the latter is sloughed off. Later another plectenchymatous layer is produced below the ascocarps and by tangential growth this may fuse at its margins with the overlying similar layer. Thus the several pyrenocarps become enclosed.

Ruhland differentiates the "primordial layer" producing the

ascocarps under the term *placodium,* and since in the case noted above it originates from the entostroma, he characterizes this type as *entoplacodial.* He traces transition stages from the entoplacodial type to his ectoplacodial type through *Diaporthe leiphaemia* (Fries) Sacc., *D. Berlesiana* Sacc. & Roum., *Endothia radicalis* (Schw.) Fries, *Fenestella* and *Cryptospora suffusa* (Fries) Tul. in which the entostroma becomes reduced and the placodium is formed in part at least from the ectostroma. In his ectoplacodial group of which *Melanconis stilbostoma* (Fries) Tul. and *Hercospora Tiliae* (Pers.) Fries are representatives, the *placodium* is formed from the ectostroma directly and the entostroma is only slightly developed.

From these latter forms it is but a step to his *haplostromatic* type in which the entostroma disappears and the perithecial initials develop within and near the base of the ectostroma. This type is represented by *Pseudovalsa lanciformis* (Fries) Ces. & de Not., *Botryosphaeria melanops* (Tul.) Wint., *Valsaria* spp., and the Xylariaceae. Both conidial and perithecial stages may be produced as in *Botryosphaeria* within the same stroma and without differentiation into special parts. He thinks these are the highest types of the Sphaeriaceae.

Traverso (75) has brought together and discussed the nomenclature of the various organs and structures found in the pyrenomycetes. He has attempted to define these terms according to their usage in taxonomic work but without consideration of their real ontogeny. He has classified stromata according to their structure and position, a method which will be helpful in systematic work provided further morphological studies warrant such applications.

Baccarini (3) has investigated a number of species which have been classed among the Dothideaceae by Saccardo and others. He concludes that there are two types of stromata: (1) spurious or *protostroma,* and (2) *sclerotiaform.* In the first he states that the perithecia have their origin either in a plectenchyma or in the case of *Phyllachora Bromi* Fuckel, *Ph. Poae* (Fuckel) Sacc. and *Dothidella fallax* Sacc., under and separately from such a stroma. In these forms developing ascogonia from a plectenchyma he also includes *Ph. graminis, Ph. punctiformis, Ph. amphidyma* and *Ph.*

melanoplaca (Desm.) Sacc. It should be noted that in these forms Baccarini considers that the dense tissue found in the epidermis and about the ostioles partakes of the character of an excipulum which is colored brown and is resistant and stratified. He thinks the stroma is digested and dissolved during the development and maturation of the perithecia.

In his second type he includes a number of species which develop a much more compact stroma such as *Scirrhia rimosa* (Alb. & Sch.) Fuckel, *Rhopographus filicinus* (Fries) Nitsch., *Euryachora Sedi* (Link.) Fuckel, *Dothidea puccinioides* (DC.) Fries, *Plowrightia Mezerei* (Fries) Sacc. and some other forms as *Mazzantia* spp. which Theissen and Sydow exclude from the Dothideales.

In *Scirrhia rimosa* the stroma forms either intracellularly in the epidermis or intercellularly between the epidermis and the sclerenchyma. In the first case the epidermal cells are broken and the lower halves of these cells remain in the interior and the upper halves form a cover for the stroma. In the second case the whole epidermis is pushed up. In both cases the outer layer becomes differentiated into a browned zone. The perithecia have their origin in the base of the stroma as clusters of delicate hyphae which by growth and dissolution form the cavity in which the asci are developed. His description of this phenomenon is not illustrated.

He concludes that in general the primordia of the ascocarps in the Dothideaceae arise independently of the reserve tissue constituting the stroma. He thinks they arise from independent filaments which twist between the cells of the stroma and remain there compressed until the moment of activity, although he cannot draw an analogy in the case of *Rhopographus filicinus* in which he says the primordia appear to arise from some of the cells of the stroma under the cortical layer. According to their method of formation, he recognizes two sorts of stromata: (*a*) those formed by aggregation of hyphae (symphogenic) and (*b*) those formed by segmentation of hyphae (meristogenic). Both types may be formed by the same fungus, as in *Dothidea Sambuci* (Pers.) Fries and *Ph. Junci* (Fries) Fuckel. He thinks the Dothideaceae correspond to Ruhland's haplostromatic types, and he believes the

group is an unnatural one which should be dropped since he is of the opinion that pyrenocarps in every case will be found to have perithecial walls.

Seaver (62) in his monograph of the Hypocreales establishes two families: (1) Nectriaceae and (2) Hypocreaceae. In the tribe Creonectrieae of the first family conidium-producing stromata are formed, the perithecia arising within them later. In the Hypocreaceae the stroma is conspicuous on a substratum or arises by a stalk-like growth as in *Claviceps* from a sclerotium, except for the genus *Hypomyces,* in which the stroma consists of a loose cottony subiculum, which is probably to be reconsidered as a loose plectenchyma homologous with stroma and has been so interpreted. Seaver's tribe Creonectrieae would be interpreted as corresponding with Ruhland's haplostromatic type.

It is a little more difficult to homologize the species in the Hypocreaceae with Ruhland's terminology. In the case of *Claviceps purpurea* the " sclerotium " is formed from the basal portion of the loose conidial structure by a hyphal growth into the ovary which becomes completely penetrated and mummified. Later this " sclerotium " gives rise to a stalk in the specialized apical portion of which the ascocarps arise. In this case the "sclerotium" is apparently homologous with Ruhland's entostroma in his diplostromatic group, though of course the conidial hymenium of *Claviceps* is much reduced and is hardly to be considered an ectostroma; or this fungus may be considered to belong to the haplostromatic group in which the ectostroma is much reduced. The stalk is to be interpreted as a structure formed from the entostroma specially adapted for spore dispersal. In the case of *Cordyceps militaris* the sclerotioid body of the insect is apparently homologous with Ruhland's haplostroma since it produces conidia and later gives rise to a specialized stalk in which the ascocarps are produced. The possible differentiation of the structures formed within the body of the larvae, into *ectostroma* and *entostroma,* should of course be considered. While it is my belief that most of those structures in the ascomycetes to which the name " sclerotium " has been applied will eventually be shown to be stromata it is manifestly impossible at present to homologize any considerable number of them with the structures described by Fuisting,

Ruhland and others since, as pointed out elsewhere, detailed morphological studies must be made upon the origin and development of may sorts of sclerotia before final judgment can be made regarding them.

Vuillemin (81) following the example of Baccarini attempts to differentiate two sorts of apparently parenchymatous fungous tissue according to their method of formation. For fungous tissues which are built up by the welding of hyphal elements he proposes the term *synenchyma,* and for similarly appearing tissues which arise by cell division in several planes the term *mérenchyma.* As examples of mérenchymatous tissue he cites the vegetative points in the rhizomorphs of *Armillaria mellea* " (Istvanffi 1891)," in the margins of the pileus of many Hymenomycetes, in the formation of the pycnidium of *Cucurbitaria Berberidis* as figured by Brefeld, in the perithecia of *Sporormia* as figured by Dangeard (1907), in the ascogones of *Penicillium vermiculatum,* and in the origin of the stroma in *Rhopographus filicinus* as described by Baccarini. The distinction breaks down he thinks in the case of *Phyllachora, Plowrightia* and *Dothidea* where he says the stromata are both synenchymatous and mérenchymatous. In my opinion the evidence presented for the existence of true parenchymatous merenchyma tissue formation in stromata is highly inadequate.

Wollenweber (84) in discussing the *Fusarium* problem defines stroma as " the bed at the base of sporiferous stages and is always present. It may be reduced to scattered hyphae, within or on the host, or it may be an aerial or immersed mycelial layer the consistency of which is either loose or plectenchymatic." He believes, however, that the stroma is of doubtful taxonomic significance.

Theissen and Sydow (73) ignore Ruhland and hold practically to the usage of Persoon. They attempt where possible to restrict the term stroma to the extramatrical as contrasted with the intramatrical portions of a fungous fruit-body, the latter being distinguished as the intramatrical stroma, often called by them the hypostroma.

For those dothidioid forms which have their stromata embedded within the host (Phyllachoraceae and Montagnellaceae in part) they differentiate " palisade-stroma " (*Catacauma biguttulatum*)

and "prosenchyma-stroma" (*Rhopographus filicinus*) though they admit that numerous intergradations are found.

Butler (loc. cit.) characterizes the fungous stromata as the mycelium condensed into pseudoparenchymatous masses irrespective of their relation to the host. He states that stromata differ from sclerotia only in their less regular shape and in having a margin less sharply delimited from the rest of the mycelium. Butler finds it difficult to restrict the term stromata, as some investigators have done, to those structures upon or within which spore-bearing organs are formed, since he wishes to regard as stromatic crusts or masses structures which are not known to produce spores, like those of *Rhizoctonia*. It seems clear however that the last had better be regarded as sclerotia although their homology with the true sclerotia of other Basidiomycetes is not apparent at the present time.

OTHER STROMA-LIKE STRUCTURES

There are further a number of structures which have been given distinctive names such as *sclerotia, xyloma, asteroma, xylostroma, astoma, tylostoma, mylitta, ectostroma, sporodochium,* and *pseudosclerotium* which remain to be considered in their relation to ascomycetous stromata. Of these structures, the "sclerotia" are the most important.

Sclerotia.—This name originated with Tode (74) who erected it as a genus with the following characterization: "Fungus simplicissimus, globoso-oblongus; substantia tenacei, duriuscula, centro demum subhiante; cortice inseparabili, superne nunquam dehiscente; fructificatione interna, ignata. *Obs.* Notis hisce genus novum a Lycoperdo fatis dispesctur." He included eight species of which it is somewhat doubtful whether any are now known as sclerotial stages of Ascomycetes. One of his species, *S. mucor,* is evidently the common sclerotium of an Agaric like those studied by Brefeld (13). His other species are indeterminable.

The name *Sclerotium* was used in the generic sense by various mycologists from Tode to the time of the Tulasnes who applied it as a common term for such bodies as the resting structure of *Claviceps.* As would be expected numerous interpretations were given. A full list of the uses of this name together with litera-

ture is to be found in Pfeiffer (59). The most common usage among the early workers was its application to the resting stage of certain Basidiomycetes. This was most natural since the one clear illustration of Tode would indicate such an alignment.

Finally the name came to be regarded in the sense of a form genus, or it was applied as a common term to any hard fungous structure which was readily separable from its substratum. In general it was regarded as possessing a brown or black rind and a medulla or central portion of closely interwoven and sometimes pseudoparenchymatous hyphal cells, often colorless. It is in this sense that de Bary and later students of the fungi have used the name, applying it with equal readiness to the large resting stages of certain Polyporaceae and Agaricaceae, for which *Mylitta* has also been used; to the asexual resting structures formed by *Botrytis;* to the small resting stages of *Corticium vagum* (*Rhizoctonia Solani*), which are only known to reproduce by mycelial outgrowths, as well as to the resting stages of a relatively large number of Ascomycetes. It seems improbable that mycologists will continue indefinitely to apply the same name to these morphologically different structures. As far as the Ascomycetes are concerned if we accept the usage of Woronin (85) for these " sclerotium " forming types we find a series of transitional stages from the diplostromatic to the haplostromatic types of Ruhland. Woronin shows for *Sclerotinia Vaccinii* Wor., *S. Oxycocci* Wor., *S. baccarum* Schroet., and *S. megalospora* Wor. a series of forms in which the conidial is well separated and differentiated from the ascogenous fructification, the former in the leaves and stems and the latter in the fruits. The conidial fructification arises from ascospore infection and the " sclerotium " from conidial infection. In these forms the conidial fructification is plectenchymatous, developing in the spring and is short lived; the ascogenous fructification develops later in the summer, is sclerotioid and passes through a long resting period until the next spring. A similar condition exists in *S. Padi* Wor. and *S. Ancupariae* Wor. according to Woronin and Nawaschin (88). *S. cinerea* (Bon.) Schroet. and *S. fructigena* Schroet. present according to Woronin (87) a well known condition in which the conidial fructification while it may occur upon the leaves and stem, is most common upon the

fruits and is developed under the epidermis as a stromatic body from which the conidia are produced by bursting the epidermal tissues. The conidial fructification here is quite compact and is more nearly like the epistroma of Fuisting. From the base of this structure the hyphae push into the interior of the flesh and build up the sclerotioid body of mixed hyphal and host tissue which later produces the apothecia as outgrowths. It seems probable as Woronin claims that the ascogone arises in a softened region of the sclerotium though more work is needed on this point. If this is the case the body though sclerotioid may perhaps be considered as homologous with the hypostroma of Fuisting which it resembles in its method of origin following the conidium-bearing epistroma. In all of these forms functional conidia of the *Monilia* type are formed.

In connection with such forms as *S. cinerea* and *S. fructigena,* it is of interest to note that Boudier (11) established *Stromatinia* as a subgenus of *Ciboria* Fuckel for those forms in which the sclerotial structure is effused and made up in part of host tissue. Later (12) he raised these forms to generic rank. Seaver and Horne (63) state that *S. Geranii* would fall under Boudier's genus *Stromatinia.* To the somewhat similar structure in the Hypocreaceae which is made up in part of host tissue as represented by *Balansia Hypoxylon* (Peck.) Atk. the name pseudosclerotium has been applied by Atkinson (2). In my opinion this is, on the basis of present knowledge, to be considered as a composite stroma comparable with Fuisting's hypostroma or Ruhland's entostroma.

In *Sclerotinia sclerotiorum* (*S. Libertiana*) as described by de Bary and in *S. minor* Godf. and *S. Libertiana* Fuckel as described by Smith (65) and Beach (7) the conidial stage is much reduced as compared with the previously discussed species. In these latter forms no functional conidia are known to be produced. Abortive (non-functional) so-called gonidia are sometimes produced from the older mycelium but the chief function of the mycelium is to build sclerotioid bodies which, after a period of rest, may produce stalked apothecia. The primordia of these apothecia have been shown in the case of *S. sclerotiorum* by de

5

Bary to originate within the sclerotial structure in the same fashion as Woronin figures for *S. Vaccinii.*

Closely related to *S. Libertiana* and *S. minor* is *Sclerotinia Geranii* described by Seaver and Horne (loc. cit.) parasitic on the rootstocks of *Geranium maculatum,* and *S. Ricini* Godf., parasitic on *Ricinus communis* as described by Godfrey (32). In both of these species the conidial stage is a *Botrytis* which is the active parasitic stage and is followed by the formation of effused sclerotioid structures which are erumpent or superficial upon the diseased portions of their host.

The other outstanding Ascomycetes which form sclerotioid structures are *Claviceps* and *Cordyceps* which were briefly referred to above. In *Claviceps purpurea* (Fries) Tul. which has been studied by Fisch (25), Tulasnes (76) and de Bary (loc. cit.) it has been shown that ascospore infection results in the production of a loosely wefted conidium-bearing structure (*Sphacelia*) upon the floral organs of rye and other grasses, especially the upper part of the ovary. From the basal portion of this structure the mycelium invades the ovary and forms the horny structure, made up in part of host tissue, known as ergot. After a period of rest this sclerotioid body puts out from its interior a stalked structure of closely appressed nearly parallel hyphae which spread out and intertwine at their apex to form a globoid head near the outer surface of which the several ascocarps are produced. This condition is slightly modified in the case of *C. microcephala* (Wall.) Tul. according to the investigations of Vincens (80), who studied the germination of the sclerotioid body and found that certain groups of cells within the compact medullary portion germinate like spores and send hyphae upward which burst the rind and form the stalk with its globoid cap in which the mature ascocarps are formed. He finds in this species that the ascogonial coils originating the numerous ascocarps arise among the growing hyphae even before the stalk has emerged through the rind. Their development proceeds along with the upward growth of the stalk and the expansion of the cap. If this is found to be the case it brings the conditions in *Claviceps* much closer to those in *Sclerotinia* where the ascogonia, as noted, arise just beneath the rind of the so-called sclerotium, and aligns the sclerotium in these cases with

the hypostroma of Fuisting (entostroma of Ruhland). Further study is certainly needed on this point both for *Sclerotinia* and *Claviceps*.

In the case of *Cordyceps* as investigated by de Bary (4, 5), Brefeld (14), Tulasnes (78), Massee (52), Vincens (79) et al., the course of development varies somewhat with the species. In general the infection of the larva is supposed to come from ascospores. The fungus penetrates the skin and ramifies more or less through the body of the insect (sometimes with the aid of internally produced conidia, *C. militaris*) until a sclerotioid body or mummy of the shape of the larva is formed. Asexual sporophores of *Isaria* or similar forms are produced from these bodies in the earlier stages but later the ascogenous stalks are produced. These may be solitary or numerous and in some species branched. In general the development of the ascocarps is supposed to be like that generally given for *Claviceps*. The development of the forms which are parasitic upon fungi as studied by Brefeld (loc. cit.), Massee (loc. cit.) and Lewton-Brain (46) appear to present no striking differences.

Xyloma.—Schweinitz (1832) used the name *Xyloma* for a tribe of the genus *Dothidea* to apply to such species as *Dothidea Ulmi. D. typhina, D. fructigena*, etc., which develop compact structures made up in part of host tissue within which the sporogenous receptacles develop, as opposed to those forms which send out sporophores or develop their ascocarps upon such a body. His *D. fructigena* on rotten apples is possibly the sclerotioid stage of *Sclerotinia fructigena*. He also uses *Xyloma* again for a subdivision of the genus *Phacidium* to apply to *Rhytisma*, etc. It is in this sense that de Bary (loc. cit.) used the term for the fructifications of *Rhytisma, Polystigma,* and *Phyllachora*. With fuller knowledge of the development of these forms this term may be found to mark significant morphological distinctions.

The terms *Xylostroma, Astoma, Asteroma, Tylostoma, Mylitta, Ectostroma* (Fries not Ruhland) and *Sporodochium* have been more or less clearly connected with one or another type of stroma-like structures but none of them in my opinion has achieved any fixed morphological significance. As our knowledge increases the

conceptions on which they are based may or may not be found to have morphological value. Their usages are outlined by Pfeiffer.

It is of interest to note that *Ectostroma* was first used by Fries as a genus of the Xylariaceae as he interpreted that family. Schweinitz also used it later for a division of *Dothidea*. Whether Ruhland was aware of these usages when he applied this name to the conidial-stroma in the *Sphaeriaceae* is not clear.

As to types of variation in the structure of stromata several have been described. De Bary used the term *pseudoparenchyma* for the isodiametric, roundish or polyhedral tissue which in section does not show its make-up of thread-like hyphae but resembles the ordinary parenchyma of the higher plants except that it is formed by a union of hyphal elements by elongation and septation and not by cell division in three planes.

Plectenchyma is a term introduced by Lindau for the porous thallus in the lichens. Ruhland applies it to the twisted more or less loose hyphal structures in the Sphaeriaceae which often later become firm (*pseudoplectenchymatous*) or even horny (*paraplectenchymatous*).

Theissen and Sydow introduce the term *prosenchyma* for a common type of tissue formed in the Dothideaceae. They say " Alle diese Formen stimmen darin überein, dass ihr Verlauf immer senkrecht-parallel-prosenchymatisch ist, nicht regellos polygonalezellig, während die Hypostromaplatten selbst neben dieser (allerdings bedeutend vorherrschenden) Struktur auch die parenchymatische aufweisen können." It is questionable whether this name, which has been applied so long to the elongated cell elements of the higher plants, should be used without modification for structures in the fungi which are so different in their fundamental nature. For such tissues formed of parallel hyphae the term pseudopalisade parenchyma may well be used.

Structurally, stromata are plectenchymatous when they are made up of more or less loose hyphae and pseudoparenchymatous when their structure becomes firmer by the welding together of the hyphae. They frequently possess an outer differentiated layer which has been called the rind by de Bary and in certain special cases the clypeus by Theissen and Sydow. This is no definite

morphological structure since it is the same in most resting fungous bodies. It may be a part of the stroma or as shown later it may be a development from the perithecium. In the case of the Dothideaceae such structures are commonly developed in the epidermal cells of the host plant and lie above, below, or on both sides of a group of pyrenocarps. Lindau's term, paraplectenchymatous, appears to apply to the sometimes hard and carbonized outer layers of true plectenchymatous stromata.

It is apparent from the foregoing that stromatic tissues have not been investigated fully enough from the ontogenetical standpoint which after all, as Goebel (loc. cit.) and Fink (24) point out, is the real basis upon which morphological conclusions should be established. It is certainly clear that the term stroma should not be used for structures developed after conjugation and built around the ascogenous elements. Stromata are regularly formed from the mycelium before ascocarp formation.

Recently a most interesting contribution to our knowledge of the Ascomycetes has been made by Arnaud (1) in his study of the Asterineae. He has brought together under this group name a large number of the tropical asterinoid fungi irrespective of their disposition by earlier workers. These interesting forms have been variously treated. They have been generally included with the Perisporiales as Lindau treated them in " Die naturlichen Pflanzenfamilien " under the family name Microthyriaceae.

Höhnel (39) working with this group noted the variation in the arrangement of the asci within the fructification which he called a *thyriothecium* and limited the Microthyriaceae to include only those forms which show the so-called " inverse radial " arrangement. This excluded a considerable number of forms with hemispherical apothecium-like fruit-bodies and led Theissen (71) to erect the order Hemisphaeriales, which he divided into three families, (1) Microthyriaceae with an " inverse radial " formation; (2) Trichopeltaceae, the shield-shaped fruit body of which is formed " pyknotisch " in the vegetative thallus as he (72) has described later in more detail; and (3) Hemisphaeriaceae, the fructification of which is hemispherical, without a thallus and not " inverse radial." The last family he divides into two tribes: (a)

Dictyopelteae (*Dictyothyrina*) with a closely netted membrane and (*b*) Thraumatopelteae (*Clypeolum*) with a pseudoparenchymatous membrane, breaking up into plates, yellow to brownish-black.

The affiliations of these rather variable Ascomycetes, many of which are parasites developing their ascocarps upon the surface of their hosts, were thought by Lindau and the earlier workers to be allied with *Meliola* and the powdery mildews on account of their superficial habit of growth and the fact that some of them develop haustoria within the host; but Theissen and Arnaud on stromatal characters think they should be considered as being more closely related to the Dothideaceae and Theissen and Sydow have included many of them in this group.

Arnaud has given us the first really adequate description of these forms together with a large number of plates illustrating the development of the radial plate-like structure overlying the asci and the position of the asci beneath. He recognizes among the asterinoid forms several types of development based on the grouping and position of the asci.

Protothyrium Salvadorae (Cooke) Arn. represents Arnaud's primitive type in which the elongated asci arise from the base of what he calls the ascus-stroma which is formed from the brown plate-like radiating structure which covers the fructification. This ascus-stroma is of course no true stroma but we need evidence as to the possible existence of ascogonia and their distribution before we can judge of its real relationships. He considers the diffused habit of the asci as indicating a primitive character and this species would then connect the Myriangiaceae with the Microthyriaceae since its radiating surface is like that of the latter family.

A similar " ascus-stroma " is found in many other asterinoid forms. True stromata of a ribbon-shaped structure are present in *Trichothyrium fimbriatum* Speg. and probably *Hysterostomella discoidea* (Racib.) Arn. where they form dense brown basal structures under the fruit bodies. The nature of the radiating asterinoid protective plates seem rather like that of the clypeus in the Dothideaceae than a true stroma. Each radiating system converges on an ostiole and thus defines the boundaries of an ascocarp.

Here and there throughout the group conidial stages appear and in *Leprieurina Winteriana* Arn. the conidial stage of *Prillieuxiana Winteriana* (Paschke) Arn., a conspicuous example is seen of the development of the stalked conidia from the inner surface of the overarching radial plate. If there is any analogy between the structures in the pycnidium and the ascocarp as is suggested from the studies of Shear and Dodge (64) on *Patellina, Leptothyrium* and *Peziza*, one might well interpret the formation of the conidia here as being further evidence of the inverse-radial development of the thyriothecium, but curiously enough the figures of Arnaud show the ascocarp of this species with the asci arising from the base and not inverse-radially.

The interesting explanation given by Theissen (69) for the development of the thyriothecium is noteworthy. He thinks that the development of the fruit body under the aerial mycelium brings about its inversion and prevents the formation of a cleistocarp with its apex toward the leaf. The result is the formation of a radial plate-like structure which is to be interpreted as the base of a flattened out pyrenocarp, the ostiole of which is formed in the center of the inverted base. The published figures of Arnaud are not very convincing as to the inverse origin of the asci. In those cases which most closely approach an inverse arrangement they appear rather to arise from the margin of the disk, and since transition stages to the cleistocarpous types are found it is pertinent to raise the questions whether the thyriothecium may not represent a pyrenocarp whose base is so flattened and spread out that the ascogenous elements are forced to the margin, or whether the margins of the disk may not produce numerous ascogones giving rise to the elements which develop downward and inward, the asci converging and turning up at their tips in order that the spores may escape through the ostiole in the center of the disk which in such a hypothetical case might be a stroma.

Certainly the asterinoid group shows some remarkable transition stages in the development of the fruit body from the thyriothecium through the apothecium-like structures in such marked forms as *Rhipidocarpon javanicum* et al. which Theissen (70) has described and figured under the name *Parmularia javanica* (Pat.) Sacc. &

Syd. as being closely related to *Lembosia,* and from these to the cleistocarp. They develop structures which are apparently analogous with those of the Phacidiaceae, Hysteriaceae and the Erysiphaceae. It is possible that further work among these forms will indicate a polyphyletic development which may throw more light upon the origin of these other groups. Inasmuch as they are chiefly tropical parasites and largely superficial in habit, the effects of their environment may have played an important part in their development. Whether they are to be regarded as primitive types of Pyrenomycetes as Arnaud prefers to regard them, or as more highly developed and specialized types are questions which cannot be answered at present. A more careful study of their degree of parasitism would perhaps throw some light on this phase of the subject.

It seems doubtful whether we can regard a majority of these types as forming stromata in the proper sense. If the plate-like structures do represent true stromata as Ward's studies would indicate, they show all conditions of epistromata, hypostromata and haplostromata. On the other hand the disks would appear to conform to Persoon's concept of stromata if we regard only the so-called " ascus-stroma " as conforming with his interpretation of what constitutes the pyrenocarp.

In the integration of the ascocarps they present interesting analogies with the conditions found in the powdery mildews though here again a number of forms are to be noted in the Microthyriaceae in which the disks of the individual ascocarps fuse to form an aggregate fructification which closely resembles the clypeus formation in *Phyllachora graminis* though of course without much evidence of being homologous.

The Meliolaceae described by Spegazzini, Höhnel and others from the tropics would appear to be closely related forms as shown especially by their mycelial and spore characters and present further interesting possibilities as to their exact position in a phylogenetic system. Stevens (66) has recently illustrated most of the Spegazzinian types. Miss Doidge (21) has called attention to an interesting form which has the mycelial and spore characters of *Meliola* but the ascocarp structure of the Microthyriaceae.

This transition which has of course been noted by previous workers serves to call attention again to the close relationship between such forms as *Asterina* and certain of the Meliolaceae which possess a cleistothecium approaching the radial type of structure as represented by some species of *Meliola*.

The problem before the student of the Ascomycetes is to interpret the various compounds or complexes of ascocarps with their matrices on morphological and physiological grounds and point out the homologies which exist. This problem must include the conidial fructifications both simple and compound since their resemblance to spermogonia as well as to ascogenous fructifications is conspicuous and in many cases ascocarps follow asexual fructifications and are combined with them in more or less complete vegetative continuity. I have endeavored (1) to review the literature pertaining to those structures to which the name stroma has been applied as well as other structures such as " sclerotia," etc., which have been more or less confused with stromata; and (2) to present observations upon certain forms of Dothideaceae whose method of development throws light on the general problem as to the morphological nature of the stroma.

MATERIAL STUDIED

The results reported are based on studies of material collected in the field during the growing season, killed in Flemming fixative, embedded, sectioned, and stained by the triple method. Two species have been given careful study, *Phyllachora graminis* (Pers.) Fuckel upon *Agropyron repens* (L.) Beauv. and *Catacauma flabellum* (Schw.) Theiss. & Syd. (*Phyllachora flabella* (Schw.) Thüm.) on *Pteris aquilina* L. Both of these are common throughout the eastern states and their relation to the Dothideaceae has never been questioned to my knowledge. They represent two distinct types in so far as stromatic characters are concerned.

PHYLLACHORA GRAMINIS ON AGROPYRON REPENS

This fungus was first described and illustrated by Persoon (56) as *Sphaeria graminis* on *Elymus europeus*. It was later transferred by Fuckel (28) to the genus *Phyllachora* of which it is the

type species. This name has been used by many mycologists
to designate almost any *Phyllachora* occurring on grasses but a
close study of the group has led me to restrict the species name
Ph. graminis chiefly to forms inhabiting members of the Tribe
Hordeae of the Poaceae. I cannot distinguish American collec-
tions of *Phyllachora* on *Elymus* spp. from European collections
on this genus of grasses by a comparison of herbarium material,
and the form on *Agropyron repens* is so closely identical that I
see no reason for separating it taxonomically from the form on
Elymus. The biological relations of these forms have not been
investigated.

This fungus matures its ascospores in the spring within the dead
leaves of its host. The first good germination of the ascospores
was obtained in May from freshly collected material. At this time
the ascospores germinate readily in a film of water upon a glass
slide. It appears to make no difference whether the spores have
escaped from the ascus or not. They appear to germinate equally
well within the ascus (Plate 8, Fig. 1a). In this case the germ
tubes grow directly through the walls of the ascus at any point.
The cytoplasm of the spore passes into the tube which grows to
a length of from three to five times that of the spores. The cyto-
plasm becomes vacuolate in the older portions of the tube and
densely granular at the tip which swells noticeably and ultimately
contains the nucleus (Plate 8, Fig. 1c). No division of the
nucleus has been observed during germination. In my cultures
the fungus develops no further in water or upon nutrient agars.
Apparently such development is dependent upon host infection.
Though more work should be done on this point it seems probable
that this fungus is a very highly specialized parasite requiring a
healthy host for its development after the habit of the powdery
mildews, rusts, etc. The few attempts to cultivate the fungus
artificially have failed, including those of Brefeld (14), and of
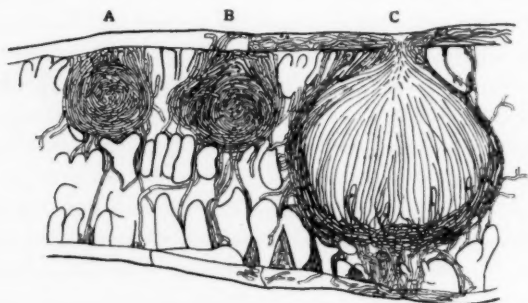Miss Dalbey (19) with the *Phyllachora* on corn.

A number of attempts were made to infect potted plants in the
greenhouse but without certain results. In no case was there any
appearance of the black carbonaceous spots resulting from these
attempts, but I have made no intensive study of infection and the
conditions favoring it.

In the earliest stages of infection which I have been able to observe the mycelium of the fungus which is from 1–1.5 μ in diameter is present more or less throughout the invaded tissues including the epidermal cells of both leaf surfaces, the palisade, spongy parenchyma and even in the vascular elements. There is a distinct tendency for the mycelium to spread most rapidly in the direction paralleling the vascular elements. This is perhaps most pronounced in the epidermal cells which are much greater in length than in width or thickness. The hyphae bore their way through the cell walls of any of these tissues. This is most readily observed in the epidermis where the walls are somewhat thicker. Here the fungus apparently absorbs a portion of the wall and passes through without any noticeable constriction. The region of the wall which is perforated does not take the safranin or orange stain, remaining colorless (Plate 8, Fig. 2). Later the parenchyma tissues of the leaf are considerably disorganized. The cells become isolated and surrounded as well as penetrated by the parasitic hyphae. Their contents slowly degenerate, the cytoplasm being replaced by globular bodies taking the safranin stain. The fixed and stained host nuclei appear as a red smear and they eventually collapse. During this process a slight swelling of the leaf tissue takes place. The hyphae tend to mass just beneath either or both of the epidermal layers. At this stage certain hyphae become slightly enlarged and rather closely septate. Coils appear which resemble in their general appearance the ascogonial coils as described for the Ascomycetes in general (Plate 8, Fig. 3). I have not been able to follow the course of development of these coils nor the passage of nuclei between the cells of the ascogonium or from an antheridium if such takes place, but it seems certain that the perithecia take their origin from these coils of hyphae.

The forming ascocarp is next observed as a ball of hyphae usually developing near the epidermis (Text fig. 1a). The mass is made up of tangled hyphae nearly uniform in diameter and so far I have not been able to differentiate the ascogenous elements at this stage.

After the ascocarp has reached a stage where it occupies about

one-third of the distance between the epidermal layers the first
evidence of color in the hyphal walls is seen. This appears in the
outer layers before the internal differentiation of paraphyses or
asci is noticeable (Text fig. 1*b*). The hyphae which are thus

TEXT FIG. 1.—Semi-diagrammatic drawing of progressive stages in the
development of the ascocarp in *Phyllachora graminis*.

A. Early stage showing penicillate structures pushing against epider-
mal cell wall. Perithecium not differentiated.

B. A more advanced stage showing early perithecium differentiation and
penetration of epidermis by penicillate structures.

C. Later stage showing parophyses; the early appearance of the asci; and
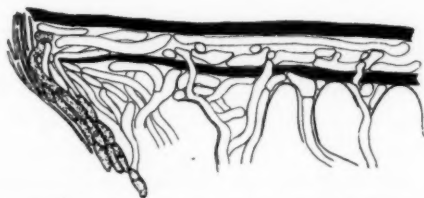the development of the clypei in upper and lower epidermal cells.

changed take on a more pseudoparenchymatous appearance, the
walls become closely cemented together and thicken slightly. This
is followed closely by the appearance of the paraphyses which ap-
parently resorb the inner hyphal mass. They develop abundantly
and come to fill the entire central region of the pyrenocarp which
has become more symmetrical and by this time fills half or two-
thirds of the distance between the epidermal layers. The young
asci are now observed pushing up among the paraphyses from
the base of the perithecium (Text fig. 1*c*).

The ascocarp continues to enlarge until it usually occupies the
entire space of the leaf parenchyma and further growth results
in a noticeable swelling or bulging of the leaf at this point and a
further disorganization of the mesophyll tissue. The maturation
of the asci and ascospores then ensures.

That a progressive formation of ascocarps takes place beginning

in the earlier region of infection and extending laterally is clear from the fact that in any median section of the functioning area the most mature ascocarps are seen near the center and the least mature at the margin of the infected area (Text fig. 1). The very early stages of ascocarp formation are to be found at the margins of the developing spot, as is generally the case in the Pyrenomycetes as well as in the Perisporiaceae.

The first evidence of the formation of the so-called clypeus is noted during the later stages in the growth of the ascocarp. At the time when the first evidence of color appears in the outer cells of the young perithecium, outgrowths of the upper layers of the pyrenocarp wall appear. These outgrowths suggest at once the well known penicillate structures whose cytological details are described by Harper (35a) in *Phyllactinia*. They form a short branched pillar-like structure over the ascocarp pushing against the lower wall of the epidermis (Text fig. 1a, b) which is then penetrated, apparently by enzymatic action (Text fig. 2). The

Text Fig. 2.—Showing a portion of an epidermal cell containing hyphae which form the clypeus; the penetration of lower wall of the epidermal cell by the outer hyphal elements of the ascocarp; the periphyses which take part in the resorption of the perithecium and the absorption of the outer epidermal wall to form the ostiole.

further lateral growth of these enlarged hyphae in the epidermal cells results in the formation of the clypeus (Text figs. 1 and 2). It usually extends well beyond the lateral boundaries of the asco-carp thus forming a roof-like structure within the epidermal cells.

The clypei of the separate ascocarps are formed progressively in any group complex. The fusion or intermingling of these lateral growths at their margins results in the formation of a continuous clypeus over the whole fruiting complex. In the same way a

continuous clypeus is formed in the lower epidermis which results
from similar downwardly directed hyphal growths originating
from the outer basal cells of the perithecium (Text fig. 1c). Thus
a group of ascocarps is protected both above and below by a car-
bonized network of stout hyphal threads often embedded in infil-
tration products. It is this structure together with the apical and
basal outgrowths from the perithecia and the fact that the pyreno-
carps are closely pressed and even fused together which suggest
the presence of a stroma in *Phyllachora graminis*. In fact, no
typical stroma is formed by this fungus so far as I have studied
it in *Agropyron repens* and *Elymus canadensis*. Further evidence
of the lack of stroma is furnished by photographs of the interperi-
thecial spaces when the perithecia are slightly separated (Plate 7,
fig. 1). It appears that the outgrowths of hyphae from the upper
surface of the perithecium are more nearly related to the "neck"
of the pyrenocarp as first described by Fuisting (29), and as a
matter of fact the clypeus of each individual ascocarp is a lateral
intraepidermal prolongation of these hyphal processes.

The invasion of the vascular elements is most readily observed
in longitudinal section. The hyphae pass into the large paren-
chyma cells surrounding the bundles and these cells are quite gen-
erally destroyed as is evidenced by the appearance of the bundles
in cross section (Plate 7, fig. 2). The similar sclerenchyma cells
and the partial starch sheath surrounding the prosenchyma are
often partially destroyed. While the phloem and xylem are not
generally directly invaded by the parasite, cases have been ob-
served where the development of the ascocarps has resulted in the
complete destruction of portions of these tissues. Such cases ap-
pear where an ascocarp is initiated in rather close proximity to the
bundles. The active elements in such cases of absorption appear
to be the hyphae which develop from the external layer of the
perithecium. These hyphae, like those which absorb the inner
wall of the epidermal cells in forming the clypeus as noted previ-
ously, penetrate readily into the xylem and phloem absorbing the
walls in part and in part growing into and filling the cells for some
distance. These phenomena of absorption, replacement and en-
gulfment are perhaps the most striking physiological character-

istics of this parasite. It is remarkable that these changes may take place without any external evidence of necrosis of the host, a feature which is quite characteristic of the group.

DEVELOPMENT OF PARAPHYSES AND ASCI

The first appearance of the filiform paraphyses in the young ascocarp has already been mentioned. They appear at an early stage and fill the perithecium quite completely. It is apparent that they originate from the inner basal layers of the young perithecium and grow upward and at the same time converge until their tips approach each other near the apex. Similar elements, the periphyses, project into the cavity from the apical portion of the perithecium. It is these structures which appear to be concerned chiefly with the resorption of the overarching membranes of the perithecium and clypeus to form the ostiole. This resorption is progressive with the growth and convergence of the periphyses but the completion of the ostiole does not take place until after the asci have begun to appear. The resorption of these outer tissues to form the ostiole is quite analogous to the ostiolar development in *Massaria* as described by Fuisting (30).

The visible development of the asci starts about the time the paraphyses are mature and the ostiole nearly or quite formed. They first appear pushing up between the bases of the paraphyses. They are binucleated at first and their development and that of the ascospores is typical of what is found in the Ascomycetes generally. Fusion followed by three divisions takes place and the spores are cut out as described by Harper and later workers. All of this development takes place in the fall although apparently the ascospores are not discharged until spring. *Phyllachora graminis* in this respect again differs from those stromatic forms in which the ascigerous development does not take place until spring.

The orientation of the pyrenocarp with reference to the epidermal surface of the host leaf is variable. Within a single group of several perithecia all kinds of orientation may be found. It seems most common to find the ostioles opening through the upper epidermis but frequently they open through the lower and in some cases through the side of the perithecial wall into the interperithe-

cial cavities when such are present. In such cases the fungus takes on the form described by Müller (53) as *Diachora* except that the asci arise from one side only of the perithecium. The explanation of these differences in orientation appears to be the position of the coiled knots which initiate them. If these arise adjacent to the upper epidermis the base of the perithecium will be near the lower and the ostiole develop in the upper surface of the leaf. The converse may take place or in rarer cases the perithecium may be placed at right angles to the usual mode of orientation and in this case it seems probable that the ascogonia arise in the mesophyll midway between the two leaf surfaces.

CATACAUMA FLABELLUM ON PTERIS AQUILINA

Schweinitz described this fungus as *Sphaeria flabella* on *Pteris aquilina* from Bethlehem, Pennsylvania. It was transferred to *Phyllachora* by Thümen and later to *Catacauma* by Theissen & Sydow (73) on the basis of the applanate stroma, formed between the epidermis and palisade layers, which is composed of densely packed pseudo-palisade parenchyma within which the ascocarps are immersed bearing paraphyses and asci said to contain simple, colorless ascospores though I have never observed them in maturity. It is found to be rather common in Pennsylvania and New Jersey and no doubt exists rather widely at least in the eastern states.

The black stromatic structure is always confined to the upper surface of the fronds and always follows the venation. Necrosis of the tissue does not result until late in the season when the fronds begin to die naturally. At this time it is noticeable that the epidermal tissues surrounding the spots turn yellow and later brown to be followed by the normal dying of the fronds.

Development of the stroma.—I have been unable to find mature ascospores of this species and have had to depend for material to show the early development of the stroma, upon sections prepared from pinnae showing the first blackening of the epidermis. In the earliest stages observed the epidermal cells and some few of the hypodermal sclerenchyma cells contain scattering hyphae (Plate 9, Fig. 1). These hyphae branch and eventually come to fill

practically all of the sclerenchyma and adjacent epidermal cells lying outside and superior to the endodermis. These hyphae are not uniform in diameter but are conspicuously vesicular and they eventually fill these cells to the point of actual distension which is most marked in the hypodermal layer of the sclerenchyma. A longitudinal section shows the sclerenchyma cells to be greatly elongated and the hyphae traversing them in a twisted irregular fashion. Interspersed among these hyphae are the degenerated remains of the host protoplast probably mixed with infiltration products of the host which in stained preparations appear as dense black or brown irregularly shaped masses.

The first rupture takes place in the hypodermal layer by absorption of the walls and probably to some extent by the physical pressure which must be considerable in this case. The hyphae within these broken cells now turn at right angles toward the epidermis pushing it upward to form the stroma and thus causing further lateral rupture. The stroma fills the cavity completely at all times by spreading laterally in a fan-shaped manner and gradually replacing the sclerenchyma and adjacent parenchyma cells of the host by absorbing them (Plate II, Fig. 2). The vascular bundles themselves are not generally invaded by the fungus. The endodermis appears to form an efficient protection through which the hyphae do not readily pass. This fungus must hence be assumed to be characteristically a cellulose or at least a cell-wall consuming organism since the sclerenchymatous cells of the host in which it lives are poorly supplied with protoplasm or included food materials.

The vertical section of the stroma is palisade-like in appearance, the cells being enlongated and nearly vertically parallel. They are well filled with cytoplasm of alveolar appearance and are typically uninucleated. The walls are tinted a faint brown but are not appreciably thickened as in the case of the fungus hyphae taking part in the formation of rind. The whole appearance is that of active meristematic tissue.

The Rind.—Judging from the fact that some of the epidermal cells are well filled with the vesicular hyphae of the fungus before the stroma is formed I must conclude that the so-called clypeus

in *Catacauma flabellum* is formed in part from these early ramifying vegetative hyphae but it is also apparent that the stromatic elements take some part in its formation. It is thus obvious that the so-called clypeus in this species presents only an anatomical resemblance to that of *Phyllachora graminis* since its origin is entirely different. This is not strange because the external layers of most carbonized fructifications among the fungi present a similar anatomical appearance. In *Catacauma* we have thus a quite different fruiting structure than in *Ph. graminis*.

The Ascocarps.—When the stroma is well formed, there appear within it at irregular intervals the ascocarps or so-called locules in which the asci and paraphyses develop. I have been unable to trace completely the development of these ascocarps. The cells of the stroma are usually uninucleated as noted. At irregular intervals I have observed giant cells which are located near the base of the stroma. These cells are at first binucleated and easily visible under the low powers of the microscope (Plate 9, Fig. 3). They appear to have arisen by the fusion of two or more cells whose contiguous walls become resorbed so that their cytoplasmic contents intermingle. Four nuclei have been observed in some of these cells and it is possible that several cells may fuse to form them. I have observed some nuclear division figures with apparently eight chromosomes present (Plate 9, Fig. 3).

In the next stage which I have observed the ascocarp is composed of a large number of small cells polygonal in shape surrounding an area in which are developing the paraphyses and the very young asci. Only by their shape and size can the outer cells of the structure at this stage be differentiated from the stroma. These cells must later be resorbed since in the more mature stages the paraphyses and asci are surrounded by a thin layer of colorless hyphae, two or three cells thick, which resemble closely the nurse tissue of the perithecium in *Ph. graminis*. These hyphae are adjacent to the cells of the stroma (Plate 9, Fig. 4). There is no definite chitinized perithecial wall such as is formed in *Ph. graminis*, but it is clear that the mature fructification is an ascocarp with a very rudimentary perithecium.

Development of the Ascus. At the base of the developing asco-

carp binucleated cells are visible and from these the asci arise in
the usual manner. Fusion takes place followed by rapid elonga-
tion of the asci which grow upward and curve inward toward the
point where the ostiole is appearing. The first division occurs
after the ascus has attained approximately its full length. This
is soon followed by the second and third division to form the
eight nuclei of the ascospores. These are usually grouped in the
upper third of the ascus rather than being scattered throughout
the ascus as in the case of *Ph. graminis*. The whole process is
otherwise like that already described for *Ph. graminis* though
spore formation does not proceed simultaneously as has been ob-
served in *Ph. graminis*. Whether there is a degeneration of some
of the nuclei in the ascus has not been determined since mature
stages have not been seen.

Ostiole.—The development of the ostiole progresses as for
Ph. graminis. The tips of the periphyses appear to be active in
resorbing the stroma above and this resorption continues through
the inner wall of the epidermal cell, on through the rind and finally
through the outer wall of the epidermis.

DISCUSSION

Notwithstanding the loose usage of the term which is common
in the literature, in my opinion the stroma is to be considered
a structure of definite morphological character which, so far as
the evidence has been presented by Fuisting, Ruhland, Baccarini
and my own studies, is vegetative in character but it may be quite
variable in structure, form and color as has been noted. It is
primarily the matrix on which or in which fructifications whether
sexual or asexual are formed. It appears also that it has other
functions as well as those of originating the conidia and ascocarps
or both. Ruhland calls particular attention to the mass action of
his "ectostroma" in rupturing the periderm of the host. He
thinks the entostroma possesses in a marked degree the property
of absorption of the host tissues which he attributes to its nutritive
activity. It may also form a firm protective covering for the asco-
carps. In addition to these functions it is apparent in *Catacauma
flabellum* that the stroma serves as a storehouse of reserve food

from which the ascocarps are to be developed after a period of rest. In this respect it takes on a function closely analogous with that of those compact forms which have been called sclerotia, but which so far as the Ascomycetes are concerned in my opinion are to be regarded as specialized types of stromata. It may be well to reserve the term sclerotium for the resting bodies formed by Basidiomycetes since it is apparent that this conforms with its earliest usage and sets them off with a distinctive name from those similarly appearing structures in the Ascomycetes. So far as the resorptive function is concerned I can see no reason for regarding it as a peculiar property of the hypostroma (entostroma). It is apparent in comparing the two widely different forms I have studied that this ability of the fungus to absorb or dissolve the host tissues is no more strongly marked in one than the other. Both are conspicuous for their ability to penetrate the cell walls of their hosts by dissolution but *Catacauma flabellum* is unique in confining itself so closely to the sclerenchyma and we must consider it to a marked degree a cellulose-consuming organism.

It appears impossible to bring all types of true stromata within Fuisting's interpretation of epistroma and hypostroma or Ruhland's ectostroma, entostroma and haplostroma for the reason that all of these terms have been applied to forms which develop first conidium-bearing stromata and later ascogenous stromata (in the haplostromatic forms the ascocarps are developed within or upon the conidia-producing stromata). Unfortunately also the derivation of these terms, with the exception of haplostroma, indicates position rather than function. In the Dothideaceae there are numerous forms which are not known to develop asexual fructifications and for these we have no means of determining whether the stromata are to be regarded as of the nature of epistroma (ectostroma) or hypostroma (entostroma). While it is apparent that many of these forms are haplostromatic in the sense of the derivation of this term, Ruhland's usage of the term implies a reduction of the entostroma as well as the assumption of the dual function of producing both conidia and ascocarps by this ectostroma. For this reason the stromata of *Catacauma* and other similar forms cannot be said at present to be definitely haplostromatic in the sense of Ruhland.

As to form and structure stromata are extremely varied. A descriptive terminology might be proposed following out some of the terms used by Theissen and Sydow but it is doubtful whether such terms would ever attain common usage. Since function rather than position seems of prime importance in designating stromata, for the present we may find such terms as *conidiostroma* and *ascostroma* useful to apply to stromata-producing conidia and ascocarps respectively, although attention should be called to two recent papers by Miss Doidge (22) in which she has used the term " ascostroma " in the same sense as Theissen and Sydow have used ascus-stroma for the bed upon which certain ascocarps rest. Without further morphological studies on the development of the forms described by Miss Doidge and others it would appear questionable whether either of such structures as the " ascostroma " and " hypostroma " which she has figured and described for *Mac-Owaniella congesta* (Wint.) Doidge and *Palawaniella Eucleae* Doidge are to be interpreted as types of true stromata. For forms which possess both sorts of stromata Ruhland's term diplostromatic is clearly applicable. Haplostroma is a useful term if we do not assume its origin from conidiostroma.

Stromata are widely present among the orders of the Ascomycetes but are apparently most generally present among the Pyrenomycetes. According to Ward's account of the development in *Dimerosporium spissum* the radiating crust formed in that and in apparently closely related forms of the Microthyriaceae is to be regarded as stromatic but Arnaud and Theissen and Sydow consider the outer crust as a cover to the " ascus-stroma " which arises variously beneath it. Certainly there can be no doubt regarding the ribbon-like stroma of *Trichothyrium fimbriatum* since this produces the disk-shaped thyriothecia. As for the thyriothecium itself we must await further studies as to the details of its origin and development before we can place a morphological interpretation upon these interesting forms.

Among the Discomycetes true stromata are present in a few cases which have been investigated and undoubtedly will be shown to be more prevalent than is known at present. Biffen (9) investigated *Bulgaria polymorpha* Wetts., already rather fully de-

scribed by the Tulasnes, and found that the mycelium formed a plectenchymatous conidiostroma in which pycnidia were first produced. These conceptacles later become filled with hyphae and a considerable further basal growth takes place. The ascogonia are developed within this structure. In *Sclerotinia* as noted two types of stromata according to their composition are formed. In *S. sclerotiorum* (*S. Libertiana*) the ascostroma is oval to kidney shaped or nearly spherical and is composed entirely of fungous hyphae. It undergoes a rest period of varying length but ultimately one or more ascogonia develop within it which give rise to the stalked ascocarps. This type is clearly analogous with that of *Catacauma flabellum*. In *S. cinerea* and *S. fructigena* the production of conidiostromata and ascostromata in close juxtaposition with the host is apparently analogous with the behavior of the diplostromatic forms of Ruhland. In *S. Vaccinii* and related forms the ascostromata when mature include a considerable portion of host tissues which have become invested, and therefore these are to be considered as composite stromata. The forms which Boudier has named *Stromatinia* may be considered as modified forms of the composite type in which the stromata are more diffused.

In the Stictidaceae the Tulasnes describe the development in *Stictis ocellata* (Pers.) Fries of a stroma which is formed in the primary cortex of its host. Further studies should be made especially in this family and that of the Phacidiaceae where in *Rhytisma* according to the Tulasnes and de Bary a well developed conidiostroma is formed and as a later development an ascostroma. Apparently these stromata correspond with Ruhland's diplostromatic forms which closely approach a haplostromatic condition. The development of plectenchymatous fructifications in *Cryptomyces Pteridis* (Reb.) Rehm which appear to be true conidiostromata and ascostromata respectively have been described by Killian (43) as forming in the substomatal and intercellular spaces of *Pteris aquilina*. Killian has been able to trace the development of the ascogonium within the already formed ascostroma and finds here a type which is perhaps similar to that described by Baccarini for *Scirrhia rimosa*.

In the Pyrenomycetes the development of stromata appears to be characteristic for the Hypocreaceae and the Dothideaceae with the probability of a few exceptions. In the Hypocreaceae the stromata in *Nectria, Polystigma, Epichloe* and *Hypocrea,* the ascosporic stage of *Aschersonia,* and close relatives are apparently analogous to Ruhland's haplostromatic types according to the investigations of Janowitsch (42), Hartig (36, 37), de Bary, Blackman and Welsford (10), Ruhland (61), Vincens (80) and Thaxter (68). In all of these forms conidiostromata are first produced and the ascocarps develop later within or upon them, most frequently near their outer surface. The development in *Claviceps* and *Cordyceps* as previously noted falls in line with the other forms except that the modification of the ascostromata, to form resting structures from which later develop the ascocarps on a stalk, is in case the ascogonia are similarly placed at once suggestive of the modifications found in *Sclerotinia.* In *Hypomyces* the loose plectenchyma in which the ascocarps originate appears to be a rudimentary conidiostroma according to the accounts of Maire (51) and Vincens. Apparently what is to be interpreted as a true stroma occurs in *Dothichloe subnodosa* as recently described by Chardon (17) although morphological studies have not been made upon this interesting form whose group relationships are not very clear.

Killian (44) has added to our knowledge of the Dothideaceae by his work on *Dothidella Ulmi* (Duv.) Winter in which he has traced the development of a conidial stroma formed of plectenchymmatous cells above the epidermis on the upper surface of elm leaves. This stroma forming a brown crust soon disappears but not before hyphae grow inward from its base to the intercellular spaces between the epidermis and the palisade cells. At this point a thick plectenchyma is formed which is divided into two types of tissue. On its periphery it is formed of irregular interlaced filaments and in the interior of isodiametrical cells. Centers of growth and consequent thickening take place within which the ascocarp initials develop by the formation of ascogonium and trichogyne. Cell fusion follows and a pairing of nuclei takes place in the ascogonium. The paired nuclei pass into the ascoge-

nous hyphae which appear soon to lose all contact with the ascogone. Killian considers the conidial plectenchyma as corresponding with Ruhland's ectostroma and the developing plectenchyma under the epidermis as analogous with the entostroma although he thinks *Dothidella Ulmi* differs from the forms studied by Ruhland in its more complete separation of the ectostroma from the developing plectenchyma beneath.

Stromata have been demonstrated in a considerable number of the Sphaeriaceae especially the Valseae, Diatrypeae and Xylariae. Among these groups the stromata are extremely variable in form as shown by Fuisting, the Tulasnes, Ruhland, Miss Dawson (20) and others. According to Ruhland there is a gradual transition from the diplostromatic entoplacodial through the diplostromatic ectoplacodial to the haplostromatic ectoplacodial type which he thinks presents the highest type of development. He infers a transition from the haplostromatic type to the Dothideaceae but such an inference is hardly justified since it is not clear that the ascocarps in this group develop within the conidiostroma as is the case in the haplostromatic forms with which Ruhland worked.

Lupo (50) has recently investigated the stromatic and perithecial development in *Hypoxylon coccineum*. He finds in the young, soft fruiting bodies four zones of differentiation: (1) an innermost central region composed of loose hyphae connected with the substratum; (2) a broad semi-circular zone above this which is composed of large, parallel, compacted hyphae; (3) a perithecial layer of loosely woven hyphae; (4) a narrow superficial layer composed of hyphae running parallel to the surface surrounded by loose hyphae which in turn is bounded by a cortical layer which he thinks was the conidium-bearing surface. While Lupo did not apparently observe the conidial stage it is inferred that it occurs over the exposed surface of the young stroma and precedes the development of ascogonia. He describes and figures the coiling of hyphae in the perithecial zone and believes these coils initiate the ascocarps. Of the large number of ascocarp initials but relatively few mature and of these a majority lie along the inner line of this zone. If Lupo's inference is correct,

Hypoxylon coccineum would belong in the haplostromatic ecto-placodial type as defined by Ruhland.

The morphological development of the pyrenocarp in *Phyllachora graminis* on *Agropyron repens* and *Elymus canadensis* is clearly homologous with that of the typical pyrenocarp with certain modifications. There is a progressive development of individual ascocarps within any infected host area beginning at the center of infection and extending outward, the successive development being more prolonged in one direction giving the mature spots an elongated shape. Each ascocarp appears to arise from a single ascogonium and develops asci, paraphyses and a perithecium. From the upper and often the lower surface of the perithecium hyphae grow which enter the epidermal cells to form the so-called clypeus. These hyphae developing from the upper surface of the perithecium appear to be homologous with the penicillate cells in the cleistocarp as well as with those forming the neck in the more typical pyrenocarp. In the case of *Ph. graminis* the neck is much reduced so that the mature fructification opens directly to the surface by an ostiole. In the progressive development of this ostiole the periphyses appear to be active in bringing about the resorption of the perithecium at this point.

The clypeus surrounding the ostiole is clearly a special structure. It is developed in a fashion more like that of the neck of the pyrenocarp, and its function is apparently that of a protective membrane.

There is no morphological ground for considering *Ph. graminis* as dothideaceous in the sense of its possessing stromata. It must be considered in my opinion as a much reduced type of the Sphaeriaceae in which all vestiges of a conidial stage have disappeared.

The perithecia develop a compact pseudoparenchymatous wall the outer cells of which are distinctly browned. By reason of the typically close proximity of the mature perithecia, their adjacent walls form within the host tissue a structure somewhat resembling a stroma, but when, as frequently occurs, the perithecia are not touching each other the lack of any dense fungous tissue be-

tween is further proof of the absence of a stroma. It is this feature which is the most reliable guide in the systematic study of dothideaceous fungi by means of hand sections, though of course one must realize that the presence of fungous tissues of various sorts in which the perithecia are embedded does not constitute morphological proof of the existence of stromata.

I find no evidence of the presence of any plectenchymatous stroma. There is in fact nothing more than the normal vegetative mycelium which falls far short of forming a plectenchyma such as Baccarini mentions for *Ph. graminis,* before the ascogonial coils are formed. Only by a comparative study of similar species can one be able to state how extensive this sphaeriaceous condition may be among the forms which have been classed as dothideaceous.

In *Catacauma flabellum* the morphological development is quite different from that of *Ph. graminis.* The enlarged irregular hyphae which extensively invade the sclerenchyma cells in the fronds of *Pteris aquilina* break out of the hypodermal cells to form a compact palisade-like pseudoparenchyma under the epidermis. I find no evidence of its origin from intercellular mycelium as described by Baccarini for *Scirrhia rimosa.* It forms an extensive, in section fan-shaped layer under the epidermis and the ascocarps arise within this ascostroma near its base apparently from the multinucleated giant cells, I have figured. Apparently, the origin of the ascocarps in *Rhopographus filicinus* may be similar according to Baccarini's rather brief account. The ascocarps in *Catacauma flabellum* are modified considerably by the reduction of the perithecium to a mere fringe of hyphal nurse cells which line the cavity in the stroma. Their delicate structure is such that it is not observed by taxonomists working with hand sections. In such preparations the ascogenous elements appear naked in the stromatal cavities.

Catacauma flabellum appears to be a highly specialized but much reduced type of parasitic Pyrenomycete in which not only has a reduction in the perithecium taken place but the conidial stage has entirely disappeared.

It is probable that *C. flabellum* represents the most general

condition existing among the stromatic Pyrenomycetes which have been termed dothideaceous, but judging from the morphology of *Phyllachora graminis,* and similar forms on grasses at least, it is evident that a considerable number of species lacking stromata have been included in this group. If we are to continue recognizing such a group it is evident that further revision is needed. Such a revision should be based on morphological grounds since it is apparent that the phylogeny of these various forms and groups can be worked out only on such a basis.

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EXPLANATION OF PLATES

PLATE 7. CATACAUMA FLABELLUM FROM PTERIS AQUILINA

Fig. 1. The same. Two ascocarps which are slightly separated showing the very definite perithecial walls and lack of stroma between.

Fig. 2. The same. Longitudinal section of leaf showing a perithecium absorbing a vascular bundle.

PLATE 8. PHYLLACHORA GRAMINIS FROM AGROPYRON REPENS

Fig. 1. *a,* Ascospores germinating in ascus. *b,* Germinating ascospore with nucleus midway in germ tube. *c,* Same, with nucleus in appresorium-like apical swelling.

Fig. 2. Cross section of epidermal cell showing penetration of hyphae through lateral walls.

Fig. 3. Ascogonial coil with two adjacent cells which are larger, more densely filled with cytoplasm and with larger, deeper staining nuclei.

Fig. 4. Portion of perithecial wall showing at left inner nurse cells. In center chitinized cells and at right the looser outer hyphal cells.

PLATE 9. CATACAUMA FLABELLUM FROM PTERIS AQUILINA

Fig. 1. Portion of the host lying above a vascular bundle showing the hyphal elements of the fungus in epidermal, hypodermal, and pericycle cells. Note the heavy walled sclerenchyma cells in center surrounded by

epidermis above, parenchyma at sides, with pericycle and endodermis below.

Fig. 2. Section of fungous stroma lying between epidermis and sclerenchyma. Note that the hypodermal layer is the one which is chiefly disorganized and broken. The epidermal cells contain the hyphae which together with abundant infiltration products (not shown) make up the so-called clypeus. The sclerenchyma cells beneath are tightly packed with the irregular hyphal elements.

Fig. 3. The same. Two adjacent giant cells showing multinucleated condition. Two nuclei in each of these cells are undergoing division.
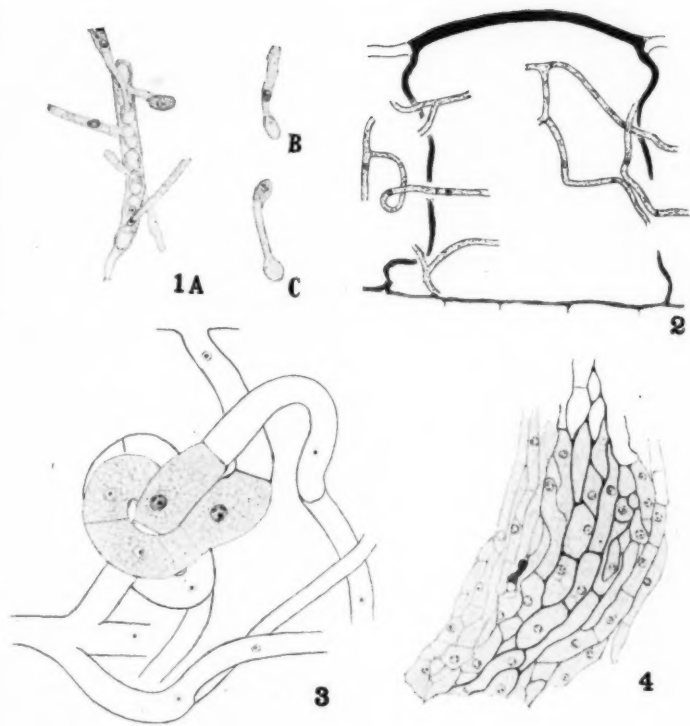
Fig. 4. The same. At left the rudimentary wall of an ascocarp bounded by the stroma on right.

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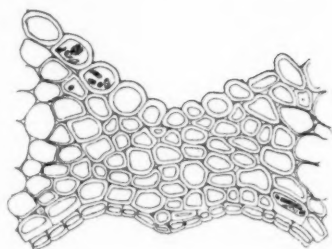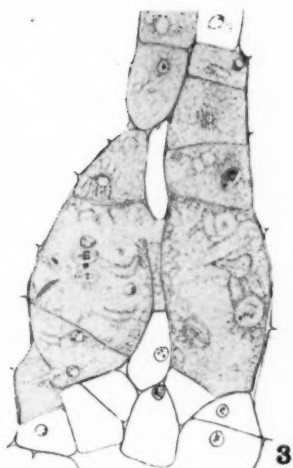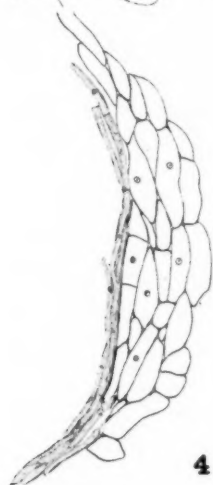
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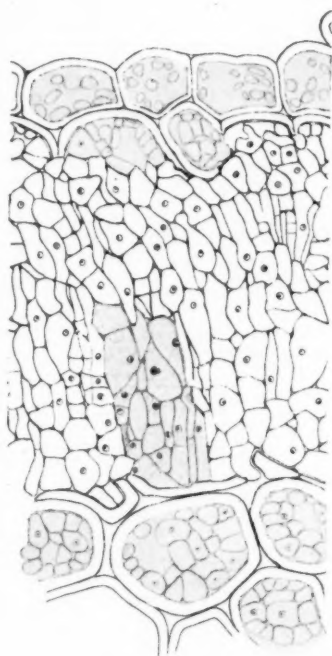
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NOTES AND BRIEF ARTICLES

LAKE PLACID FUNGI

The fungi listed below were found in the Lake Placid region, October 19–25, 1923, while the writer was enjoying a brief vacation at the Lake Placid Club. On a previous visit in October some years ago, the ground was covered with a light snow but the weather last fall was sunny and rather warm during the day with several frosty nights. The first frost of the season dated back to August 15. For a brief popular account of the vegetation in general at Lake Placid, the reader is referred to an article contributed to the current volume of the *Journal of the New York Botanical Garden.*

Puffballs were rather scarce, only three species being found, the commonest being *Lycoperdon gemmatum.* The cup-fungi were represented by *Helotium citrinum,* a late species; the slime-molds by *Lycogala epidendrum;* the gelatinous fungi by *Exidia arborea* and *Dacryomyces aurantia;* and the semi-gelatinous forms by *Merulius tremellosus,* seen in abundance on a sugar maple stump. Resupinate forms were common, especially on the underside of logs and fallen branches, where they were protected by the warmth of the earth. Several species of *Stereum, Hymenochaete, Corticium,* and the other Thelephoraceae were found on dead wood, as well as resupinate polypores. *Fuscoporia ferruginosa* was frequently seen, and *Fomitiporia prunicola* was common on dead trunks of Pennsylvania cherry trees that had been killed by it.

This region is an excellent one for polypores, because of the immense amount of fallen timber of various kinds and the prevailing moist conditions. Many of the living trees bear large brackets and without doubt considerable damage is done by the tree-destroying species. *Pyropolyporus igniarius,* for example, was abundant on birch, beech, elm, maple, hop hornbean, and other

hardwood trees. *Elfvingia megaloma* attacked a wide variety of hardwood trees—even cottonwood—and formed brackets reaching two feet in diameter. Coniferous trees were found attacked by the thin forms of *Porodaedalea Pini* and *Fomes roseus,* and the hoof-shaped *Fomes ungulatus.* *Coltricia tomentosa, Coriolus abietinus,* and *Gloeophyllum hirsutum* were also found on coniferous wood; and *Tyromyces chioneus, Irpiciporus lacteus, Polyporus Polyporus, Bjerkandera adusta, Daedalea confragosa,* and several species of *Coriolus* on hardwood. *Coriolus versicolor* and *C. pubescens* were more common than *C. prolificans* and *C. nigromarginatus.* The darker, zoned form of *C. pubescens,* which is the typical European form, was common on dead aspen and other hardwoods; while the white, scarcely zonate form with long hairs and long, thin-walled tubes was found once in dense masses on sugar maple.

The number of fleshy gill-fungi was undoubtedly much reduced by the unusual drought of the past season. Those I found were mostly in moss or thick humus in the dense shade of coniferous trees. Some appeared to be summer or early autumn species that were lingering into fall, but were neither abundant nor happy. Among these were: *Marasmius oreades, M. rotula, Laccaria laccata, Gymnopus dryophilus, Russula emetica, Cortinarius armillatus, Lactaria theiogala, Lactaria ocellata, Crepidotus mollis, Geopetalum abietinum, Gymnopilus penetrans, Hypholoma capnoides,* and *Paxillus involutus.* Others appeared to thrive under such conditions. *Gymnopus velutipes,* the winter mushroom, was in its glory but not common. *Chanterel aurantiacus* never appeared more beautiful than when growing fresh from coniferous stumps in the forests about the lake after a slight rain. *Omphalopsis campanella* appeared by the hundreds on balsam and spruce logs that were badly decayed. *Hypholoma sublateritium,* better known to Americans as *H. perplexum,* was not rare on dead hardwood timber; while *Crepidopus serotinus* appeared in conspicuous imbricate masses on living sugar maple trunks, and rarely on birch and certain other trees.

Moss-loving species that seemed to love frosty nights were: *Hygrophorus hypothejus, Chanterel muscoides (C. dichotomus*

Peck), *Lepiota amianthina, Cortinellus vaccinus,* and one or two
species of *Cortinarius* that I have not yet determined. *Clitocybe
dealbata* grew on the shaded borders of the golf links where I
had seen it frequently before; but I was surprised to find large
masses of a species similar in appearance, habit, and habitat, al-
though very much larger and more abundant, growing in the
grass in several places about the old summer hotel. When I find
the time to study it, this may prove to be a very interesting species.

<div align="right">W. A. MURRILL</div>

The fifteenth annual meeting of the American Phytopathological
Society was held at Cincinnati, Ohio, December 27–January 1,
1924. The following abstracts of papers presented are copied
from those published in advance of the meeting.

Chestnut blight in Europe (Endothia parasitica (Murr.) A. & A.). HAVEN
    METCALF.

The occurrence of chestnut blight at Bruges, Belgium, is reported.
It is believed that this is the first report of this disease in Europe. In
London a chestnut staging-pole was observed with a blight canker on it,
but the fungus was dead. The theory is advanced that the chestnut blight
may have been taken to Europe from America on chestnut poles or other
chestnut timber during the war.

Fungous diseases of the China aster. W. O. GLOYER.

The following parasitic fungi on the China aster were studied:
Ascochyta asteris (= Phyllosticta asteris Bres.), *Botrytis cinerea, Coleo-
sporium solidaginis, Fusarium sp., Phytophthora sp., Rhizoctonia solani* and
Septoria callistephi. The leaf spots caused by Ascochyta, Botrytis, Coleo-
sporium and Septoria were controlled by spraying with Bordeaux mix-
ture. Ascochyta Botrytis, Fusarium and Septoria are seed borne and
seed treatment with mercuric chloride proved more practical than spray-
ing the plants. Botrytis, Fusarium, Rhizoctonia and Septoria may cause
damping off and stem rot. Septoria is viable on two-year-old seed. As
Septoria and other fungi winter on the stalks, they should be burned.
Asters are susceptible to the other diseases studied during the seedling
and seed producing periods, but the plants are attacked by Fusarium and
Septoria at any period of their growth.

Poria cocus developed on tuckahoe found attached to orange tree root.
GEORGE F. WEBER.

Several tuckahoes were found, in June, 1923, attached to the roots of
an orange tree near Gainesville, Florida. They varied in weight from 5
to 9 pounds and were irregular in shape. The outside covering was bark-
like, brown and tough. It varied from 3 to 8 mm. in thickness. The
inner texture was white, starchy, spongy and gave off a mushroom odor.
One of these bodies was sterilized for twenty minutes in a 1–1000 solu-
tion of corrosive sublimate. It was then carefully washed in five changes
of sterile distilled water and placed in a sterile moist chamber at room
temperature exposed to intermittent light. After ten days a chocolate-
brown fungus growth appeared in several places on the outside cover-
ing, this growth matted down and fruiting structures developed of a
resupinate nature apparently that of a Poria sp. The pores were irregu-
lar, 2 to 4 mm. deep, and of a distinct chocolate-brown color. The
basidiospores were greyish white 6–9 × 2–4 μ.

The grey bulb-rot of tulips. H. H. WHETZEL AND JOHN M. ARTHUR.

This disease long known in Holland and Germany as the sclerotium
disease of tulips is here reported apparently for the first time from
America. The identity of the pathogene with the fungus described by
Klebahn as *Sclerotium tuliparum* has been established. A critical study
of the fungus indicates that it is a Rhizoctonia rather than a Sclerotinia
as suggested by Klebahn. The organism is therefore transferred to the
former genus under the name *Rhizoctonia tuliparum* (Klebahn) nov. comb.
No perfect stage has been discovered.

Soil disinfection experiments made in October, 1923, indicate that the
fungus may be effectively eradicated from infested soil by the applica-
tion of formaldehyde solution at the rate of 1 lb. (40 per cent.) formalin
per 5 square feet of soil surface. The drench used was made up at the
rate of one part formalin to fifty parts water and was applied 12 plates
by variations in the rate of growth, production of conidia and aerial
hyphae, and shape and elevation of the colony.

Two bacterial diseases of gladiolus. LUCIA McCULLOCH.

An undescribed leaf blight, particularly destructive to young stock,
has been found on several varieties of gladiolus. The spots are trans-
lucent, usually angular, water-soaked, dark green, becoming brown.
From these lesions there is a copious bacterial exudate in which soil
particles become imbedded.

The organism, which produces a yellow, viscid growth on culture
media, has been isolated repeatedly, its characters studied and its patho-
genicity proved. The group number is 211.2322523. The name proposed
for this organism is *Bacterium gummisudans*. A complete description of
this disease has been submitted for publication.

The other disease, caused by *Bacterium marginatum* L. McC., was re-

ported briefly in Science, August 5, 1921, as a rot occurring at the base of gladiolus leaves. Further study demonstrated that this organism is also the cause of a characteristic disease of gladiolus corms. Husk lesions are brown to black, causing holes or cracks. On the body of the corm the spots are circular, depressed areas, yellow to brown, horny in texture, easily removed, leaving clean saucer-shaped pits. In these lesions of husk and corm the bacteria remain viable and pathogenic from season to season, thus providing a source of infection wherever the diseased corms are planted.